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**STUDIES ON MONOSTOMES
A — THE DIGESTIVE SYSTEM**

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY
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I. INTRODUCTION

More than a century ago the first of the Monostomata were discovered and described. Since that time the literature on this group has become extraordinarily abundant. Many of these works however serve only to make profound chaos. Parasitologists have given little attention to the study of this group in North America. Although as early as 1856 Jos. Leidy found and named monostomes from North American birds his descriptions are so brief that it is impossible to determine from them a single species. It is only in more recent years that members of this group have received more serious and more precise study.

It is the purpose of the writer in this paper to give a detailed description of the digestive system as derived from a careful study of many specimens of the material at hand which is listed below. Dwelling at some length on the oral sucking apparatus found in two species of the genus *Cyclocoelum* and to show as clearly as possible its relation to the polyphyletic origin of the Monostomata.

Material - The material used for these observations was obtained principally from the collections of Professor Henry B. Ward. These consist of various specimens of *Cyclocoelidae*, *Notocotylidae*, *Heronimiidae* and *Collyriclidae*.

The *Cyclocoelidae* consists of collections from various parts of the United States; Nanking, China; and Chiangmai, Siam. Among these collections the following species were found.

Cyclocoelum VN 94.1 from the abdominal cavity, probably the abdominal air sacs of *Totanus melanoleucus* (Gmel) collected by W. C. Hall, April 7, 1894. The locality while not stated is pro-Creston, Iowa.

Cyclocoelum VN 95.1 from *Totanus solitarius* (Wils) taken at Creston, Iowa by W. C. Hall August 18, 1895. The organ of the host is not stated.

Cyclocoelum VN 95.2 from the air sacs of the abdomen of *Tringa maculata* (Vieill) taken by W. C. Hall at Creston, Iowa, September 4, 1895.

Cyclocoelum VN 08.180 from the lung along the back and in the abdomen of the Straight Billed Curlew, *Limosa fedoa* (Linn) collected by W. E. Allen, Long Beach, California, October 1, 1900.

Cyclocoelum VN 08.179 collected from *Symphaemia semipalmata* (Gmel) at Lincoln, Nebraska, August 28, 1900. Organ of the host and collector unknown.

Cyclocoelum VN 08.172 from the abdominal cavity of *Gallinago delicata* (Ord). Locality of the host and the collector unknown.

Cyclocoelum VN 1041 from the lung of a wild duck, species unknown, collected by C. E. Stringer at Omaha, Nebraska, April 1903.

Cyclocoelum VN 15.65 from the magpie collected by R. T. Shields, at Nanking, China, 1915. The organ of the host unknown.

Cyclocoelum VN 19.26 collected from the liver of *Gallinago delicata* (Ord), taken at Chiengmai, Siam, Jan. 1, 1918 by M.E. Barnes.

The Notocotylidae consists of *Notocotyle quinqueserialis* Barker and Laughlin 1911. Collected from the intestine of the Muskrat, species unknown.

Catatropis VN 16.428 from the intestine of the Muskrat, species

unknown, taken at Wray, Colo. by C. H. Gable, October 30, 1916.

The Heronimiidae of *Aorchis extensus* Barker and Parsons 1914, VN 12.162 from the lungs of *Emys blandingii* taken by R. G. Hall at North Judson, Indiana, August 17, 1912.

Aorchis VN 17.27 collected by T. B. Magath from the lungs of *Emys blandingii* taken at Fairport, Iowa, 1917.

Aorchis from the lungs of *Chrysemys marginata*, taken at Urbana, Illinois, and Muscatine, Iowa, June 1918, collected by the writer.

The Collyriclidae consistsof, *Collyriclum colei* Ward, VN 11.11 and 11.12, collected by Leon J. Cole from *Passer domesticus* taken at Madison, Wisconsin, June 18, 1910

Collyriclum colei Ward, collected from cysts in the subdermal tissue of *Passer domesticus* taken at Ripon, Wisconsin, July 1907.

The above specimen is number 14.515 of the National Museum collection. For the loan of this the writer is deeplu indebted to Professor Henry B. Ward through whose influence it was secured.

The writer wishes to take this opportunity to express most sincere thanks to Professor Henry B. Ward for the loan of the greater part of this material, and for his profound interest shown throughout the progress of this work, deepest apprediation.

Methods - The methods used in preparing this material for study were those ordinarily used with such material. No special technique being requized. In general sections were stained in toto with Erlich's acid hematoxylin with a counter stain of alcoholic eosin. Sections were cut 10 to 20 micra in thickness. Frontal, sagittal, and transverse sections were used. In order to obtain a clearer perception of the more minute and obscured parts wax reconstructions were made. These were employed particularly to find the relationship and constancy of the female genital organs. For helpful sug-

gestions regarding the technique of modeling in wax the writer wishes to express here deep gratitude to Professor J. S. Kingsley.

II. THE DIGESTIVE SYSTEM

Oral sucker - Von Siebold (1835) the first to give a clear account of the anatomy of the Monostomidae in his description of *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) speaks of the mouth as a transverse oral opening leading to a funnel formed canal which narrows gradually posteriorly and terminates in the "so-called" pharynx. No trace of a sucking organ was observed.

Following this Van Beneden (1850) refers to the above work frequently, but states that the monostomes have only a mouth sucker situated in the anterior region. In another paragraph of this same work he speaks of the digestive system of Trematodes as showing generally an anterior sucker in the bottom of which is situated the mouth. This he says opens into a second enlargement similar to the preceding sucker, the pharyngeal bulb. In his figures of *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) the structure termed pharyngeal bulb above is indexed as buccal bulb. These show the pharyngeal bulb with no anterior sucking musculature surrounding the mouth opening. In a later paper (1861) describing again this same species he speaks of the bulb and the region preceding it which he says is seen with difficulty. A little later in this work in the description of *Notocotyle* (*Monostomum*) *verrucosum* he ventures to use the term "La ventuose antérieure ou plutôt le bulbe buccal", applying it to the spherical muscular bulb at the extreme anterior of this worm, a Notocotyloid, evidently mistaking this structure for the same structure termed the pharyngeal bulb in the earlier work. His descriptions show clearly that the same organ which in the distomes is termed pharynx is here termed anterior sucker or buccal bulb.

Some years later Monticelli (1892) described the mouth as small in *Monostomum mutabile* and *Monostomum expansum*; of greater or less size in *Ogmogaster plicatum* and *Monostomum galeatum*; circular in *Monostomum hippocrépis* and *Monostomum trigonocephalum*; ellipsoidal in *Monostomum cymbium* and *Monostomum ornatum*. Usually ventral and generally situated in the extreme anterior. When present a prepharynx of variable length situated directly in front of the pharyngeal sucker, anterior sucker or buccal bulb of Van Beneden. Monticelli here differentiates the region described by von Siebold (1835) as a funnel formed tapering canal from the adjoining posterior structure. This structure which was described by both von Siebold (1835) and Van Beneden (1850 & 1861) is here termed a prepharynx. He says that in *Notocotyle* and some other genera of this family the prepharynx is wanting and that then the pharynx is anterior and serves the role of an anterior sucker for this reason he designates this structure in these genera as a sucker pharynx.

Braun one year later refers to the description of Monticelli and proposes that a sucking organ will be developed out of the pharynx. In 1901 the same author refers to the *Bulbus buccalis* of Van Beneden, pharynx of Monticelli as a "Mundsaugnapf" which he says is followed by the oesophagus. In another paragraph of the same work when describing *Monostomum trigonocephalum* Rud. since removed by Looss to the genus *Pronocephalus*, collected from the intestine of the Sea Turtle he says that the sucker is 0.12 mm long and 0.09 mm broad and again stated that it is followed by a straight oesophagus 0.3 mm long, without a pharynx. Thus Braun has construed the muscular structure at the extreme anterior in the *Notocotylidae*, *Pronocephalidae* and other families of this group to be a development of a structure similar to that termed pharynx by Monticelli in

the Cyclocoelidae.

Barker and Laughlin (1911) accepts this view without comment and describes the worms, *Notocotyle quinqueserialis* Barker and Laughlin (1911), as clinging to the intestine of the muskrat tenaciously with the well developed oral sucker. They found no evidence of a pharynx (Monticelli).

Taschenberg (1879) describes the mouth in the genus *Didymozoon* as an opening followed by a funnel formed duct leading to the pharynx (Monticelli). This he states to be generally characteristic of the entire group. Lönnberg (1891) found in *Didymozoon lampridis* the well developed sucker, pharynx of Taschenberg, and just posterior to it a very small muscular bulb the pharynx. Odhner (1901) finds in *Didymozoon scombri* Tschbg. a similar pharyngeal bulb which he figures and proves beyond doubt that the pharynx of Taschenberg is a very strongly developed sucker followed by an extremely small pharynx. In this same notable work he says that in *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) and other parasites where only a pharynx (Monticelli) is present that there is always a region anterior to it which he terms "Mundrohr" or "Mundhöhle" prepharynx of Monticelli a structure which by the contraction of the inner walls changes the pharynx into a sucker. This same region is shown in the figures of Odhner for *Didymozoon scombri* Tschbg.

Looss (1899) speaks of the mouth sucker but gives no equivalent for the pharynx of Monticelli. Later however he interprets the swelling at the beginning of the oesophagus in *Microscapha reticularis* as a pharynx. Cohn (1904) calls this to account when he states that this swelling is nothing more than the oesophageal sphincter which is present in many species. The same author interprets the mouth sucker of Looss, buccal bulbe (anterior sucker) of

Van Beneden as a pharynx (Monticelli) and adds that it is his opinion that soon monostomes will be seen with a well formed sucker adjoining a typical pharynx. The evidence given in support of this consists of the statement that *Haplorchis cahirinus* Looss has a strongly developed pharynx preceded by a rudimentary sucker and that he has observed in *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) and in one other species (to be published later) a rudimentary sucker. On the contrary Looss (1899) figures *Haplorchis cahirinus* with a well developed but small oral sucker followed by a somewhat smaller but perfectly developed pharynx and in his description of this species states specifically that the oral sucker and the pharynx are well developed structures. The rudimentary structure occurring on the ventral side as an acetabulum, (Bauchsaugnapf of Looss). He adds also that the nerve commissure, which according to Braun, M. (Cohn 1902:715) lies, in all the Digenea more or less bent around the dorsal side of the oral acetabulum and the pharynx and is in front of the muscular sucking organ in the Monostomidae and therefore that organ is a true pharynx. This organ serving both as a sucker and a pharynx.

Stossich (1902) calls the pharynx (Monticelli) an "inner sucker" which he says serves the same function as the mouth sucker of the other trematodes.

Odhner (1907) states that those that acquire holdfast organs in the least degree are the parasites of the respiratory organs; the group containing *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) being intirely suckerless.

Kossack following the decision of Monticelli says that the question can be determined only by a study of the position and distribution of the nerve ganglia. Consequently he termed the

anterior muscular structure a true pharynx. Ward (1918) calls the same structure the oral sucker and states that no pharynx is present.

The interpretation of Braun, Looss, Ward and others is indeed well exemplified in many cases where the anterior region is telescoped posteriad over the opened anterior portion of the pharynx (Monticelli) (Fig. 9).

In the light of the foregoing the question brought out by a long continued controversy remains unsettled. Is the structure termed the pharynx by Monticelli (1892) phylogenetically a pharynx or an oral sucker? While Monticelli (1892) attempted to prove by the distribution of the anterior nerves that the muscular bulb (pharynx Monticelli) was a true pharynx this has not been generally accepted and hence remains a matter of much controversy. In the opinion of the writer the brain commissure which lies distinctly anterior to the pharynx (Monticelli) (Fig. 2) can be used as a land mark only and in a different state of contraction might have its relative position changed and that the innervation is no doubt distributed to the other anterior structures as well. Although the nerve commissure has the same relative position in the distomes this alone does not prove the phylogenetic origin of the pharynx (pharynx) and that when a muscular sucking apparatus is found and proof established for such an organ anterior to and adjoining the pharynx (Monticelli) as predicted by Cohn (1904) then and only then can these organs be safely determined as oral sucker and pharynx (Monticelli).

In this study the writer has examined more than 100 specimens of the genus Cyclocoelum Brandes (Monostomum Zeder) comprising at least five different species. In this material three different conditions are found.

In Cyclocoelum VN 19.26, VN 94.1, VN 08.179, VN 08.183, VN 95.1 and VN 95.2 no trace of an oral sucker as it generally occurs in the distomes is found. In these the prepharyngeal structure is characterized by the following description.

The structure of the prepharynx (Monticelli) is characterized by the following and is the typical condition in the above named species. The mouth opening is at the extreme anterior end of the animal on the ventral side of the body. The dorsal side of the body projecting over the ventral as a protecting shelf. This shelf or labium has two slight grooves on the ventral surface separated by a more or less prominent ridge. At the crest of these grooves the cuticular layer of the body wall becomes thin (Fig. 4). At the posterior edge of the labium where the mouth opening forms a circular outline, the longitudinal and oblique muscular layers of the body wall disappear and the circular layer is very much reduced from that which one finds in other parts of the body wall. This leaves only a light circular muscular band suspended by the transverse muscle strands (Fig. 4). There is no evidence of any outer circular muscular band as is characteristic of the suckorial organs in the distomes and those of Cyclocoelum to be discussed later. This structure in these species agrees well indeed with the structure so fittingly described by von Siebold (1835) and Van Beneden (1850) and named prepharynx by Monticelli (1892). One would expect a prepharynx to be a simple tube leading to the pharynx and in these forms this duct fulfills all of the conditions laid down by Monticelli (1892) with regard to this structure.

On the contrary in Cyclocoelum VN 10.41 an intermediate condition is found. In this species the labium extends forward as in the case just described. The cuticula leaves off in a similar man-

ner but in this case the longitudinal and oblique muscles are actually increased immediately surrounding the buccal duct which leads inward toward the very muscular pharynx (Fig. 5). From this more or less muscular wall, radial muscles extend outward having their origin in a weak band of circular muscles. This outside covering of the sucker is held in place by the transverse muscles in the same manner as the sucker of the distomes.

Were this the only case found one could perhaps accept Cohn (1902:715) who has observed what he terms a rudimentary mouth sucker in *Cyclocoelum mutabile* (Zeder).

The maximum condition observed by the writer was found in *Cyclocoelum* VN 15.65. Here the labium projects anteriorly as in the cases described previously (Fig. 10). Posterior to the opening of the mouth which is downward as before a large weak oral sucker scarcely visible in toto preparations is seen. It is from one-third to one-half larger than the pharynx posterior to it and extends from the extreme anterior of the animal to well over the anterior portion of the pharynx. It measures 0.314 mm in length by 0.463 mm in width. The musculature is much less strongly developed than that of the pharynx and consists of an outer circular layer connected by radial, longitudinal, and oblique muscles to a much heavier inner circular band which forms the muscular walls of the mouth. (Figs. 6 & 7). This muscular body is suspended by much lighter strands of transverse muscle having their origin in the musculature of the body wall and their insertion one time in the outer circular band of muscles covering the sucking musculature and again in the radial muscles of the sucker itself. (Figs. 6 & 7).

In general the position of this sucker is such that it opens downward but suspended as it is a slight contraction of the dorsal

suspensory muscles and at the same time a relaxation of the ventral ones could easily give to the sucker a different position so that its aspect would be changed from that of its true antero-ventral one (Fig. 8).

Following the oral sucker is a thin walled slightly muscular tube extending posteriorly ventrad to the pharynx and opening into it on the ventral side. The writer believes this to be a condition due to the state of contraction at the time of preservation and that in a fully extended specimen the oral opening would enter the pharynx from the anterior thus leaving some 150 to 200 micra between the oral sucker and the pharynx. This portion is termed the prepharynx (Fig. 10).

As will be seen by the description which is to follow later the structure of the pharynx (Monticelli) is practically identical in many of the species of this and other families and therefore must necessarily have developed from a similar tissue in a similar manner, both in the species with and without the anterior muscular sucking structure. This being the case there remains the functional differentiation which may come about in the absence of the sucking structure. No doubt the pharynx (Monticelli) functions as a sucker in drawing in food and it is highly probable that the suction produced by these heavy muscular walls is indeed very great. And as was stated earlier in this discussion the position of the oral sucking apparatus relative to the pharynx in both those species with and those without the true oral sucking apparatus (Fig. 9) strongly indicate this view.

As was stated before the muscular bulb, pharynx of Monticelli, is identical in structure and has no doubt arisen in the same manner in all the species of this family. Even though it may function

as a sucking organ in some instances this structure has not been modified and does not appear to be typical sucker tissue as it is described in the distomes. If however this muscular organ is present in one or more species of this genus at the same time with an anterior musculature which is typical of that tissue as found in other groups of trematodes and is constant in those species then one is justified in designating the anterior musculature a sucking organ or oral sucker and the musculature posterior to it a pharynx as termed by Monticelli (1892).

The Pharynx - Immediately posterior and dorsal to the pre-pharynx is the strongly muscular bulb which appears to be a muscular structure developed around the wall of the posterior pre-pharynx or anterior oesophagus. On first observation the pharynx appears as two bean shaped halves lying one on either side of the anterior portion of the oesophagus. On more careful study however it is found to consist of heavy muscular halves bound together on the edges by smaller bands of fibers so that in the true cross section it appears as a cylinder with an elongated dorso-ventral slit passing through it.

The pharynx is variable in size and form, within the species as well as in different species, and may be in some species distinctly elongated while in others it is noticeable expanded laterally and still in others it is spherical. It measures in *Cyclocoelum* VN 10.41, 0.778 to 0.910 mm in length by 0.745 to 0.844 mm in width. In *Cyclocoelum* VN 08.179 and VN 08.183 it is in general spherical and measures 0.231 to 0.298 mm in length by 0.182 to 0.264 mm in width and 0.215 to 0.248 mm in length by 0.198 to 0.248 mm in width respectively. In *Cyclocoelum* VN 08.180 it is distinctly longer than broad and measures 0.264 to 0.314 mm in length by

0.198 to 0.248 mm in width. In Cyclocoelum VN 15.65 the pharynx is slightly oblong measuring 0.264 to 0.331 in length by 0.215 to 0.281 mm in width.

While the range of measurements gives a general idea of the size and shape it will be seen from the following table that the individual which has the longest pharynx is not always the one which has the narrowest one and vice versa.

Table I. shows individual measurements for the lots mentioned above and here will be seen the variation as shown by representative specimens.

Name	Measurements in mm.											Average	Range
	1	2	3	4	5	6	7	8	9	10	11		
<i>Cyclocoelum</i>	L 0.778	0.910	0.794	0.824								0.827	0.778-0.910
VN 10.41	W 0.778	0.844	0.745	0.778								0.786	0.745-0.844
<i>Cyclocoelum</i>	L 0.264	0.298	0.264	0.231	0.248	0.248						0.259	0.231-0.218
VN 08.179	W 0.264	0.182	0.215	0.231	0.198	0.215						0.217	0.182-0.264
<i>Cyclocoelum</i>	L 0.248	0.215	0.215	0.248	0.231	0.231	0.248	0.215	0.231	0.215	0.231	0.230	0.215-0.248
VN 08.183	W 0.248	0.215	0.248	0.248	0.198	0.231	0.248	0.215	0.231	0.231	0.231	0.231	0.198-0.248
<i>Cyclocoelum</i>	L 0.281	0.298	0.264	0.281	0.264	0.264	0.264	0.314	0.314			0.283	0.264-0.314
VN 08.180	W 0.248	0.248	0.215	0.248	0.198	0.248	0.231	0.248	0.248			0.237	0.198-0.248
<i>Cyclocoelum</i>	L 0.281	0.331	0.264	0.314	0.298							0.297	0.264-0.331
VN 15.65	W 0.248	0.281	0.215	0.248	0.248							0.248	0.215-0.281

Table I. - Showing variation in the length and width of the pharynx in 5 different species of the genus *Cyclocoelum*.

The above table shows at a glance that the size and form of the pharynx is not constant as might be indicated by an average or range. Cyclocoelum VN 08.183 shows eight instances in which the pharynx was round, two with a greater width than length, one with a greater length than width. Giving an average for eleven specimens of 0.230 mm in length and 0.231 for the width, hence by this count of a greater width than length while eight of the eleven cases cited show the pharynx to be spherical. From the range one could infer from the maximums that the pharynx is spherical but from the minimums of less transverse diameter than longitudinal. In VN 08.180 and VN 15.65 (Fig. 8) every specimen measured showed a greater length than width while in VN 10.41 and VN 08.179 some were spherical while the majority have a greater length than width. From this comparison one sees readily that the pharynx possesses such variability in size and form in this genus that it can be termed at least only spheroidal.

The musculature of the pharynx is, as stated previously, similar in all the species of this genus and consists of numerous fibers bound into bundles that are so interlaced as to make a very powerful organ and in the absence of the oral sucker it is quite probable that it serves as a sucking organ as was stated earlier in this work.

The musculature is quite characteristic of this organ as it is found in the distomes and consists of circular, radial and longitudinal fibers. The circular muscles are most numerous of all and constitute approximately 75 per cent of the entire structure (Fig. 9). This is pierced by bundles of radial muscles which have their origin in the outer layer of circular muscles and their

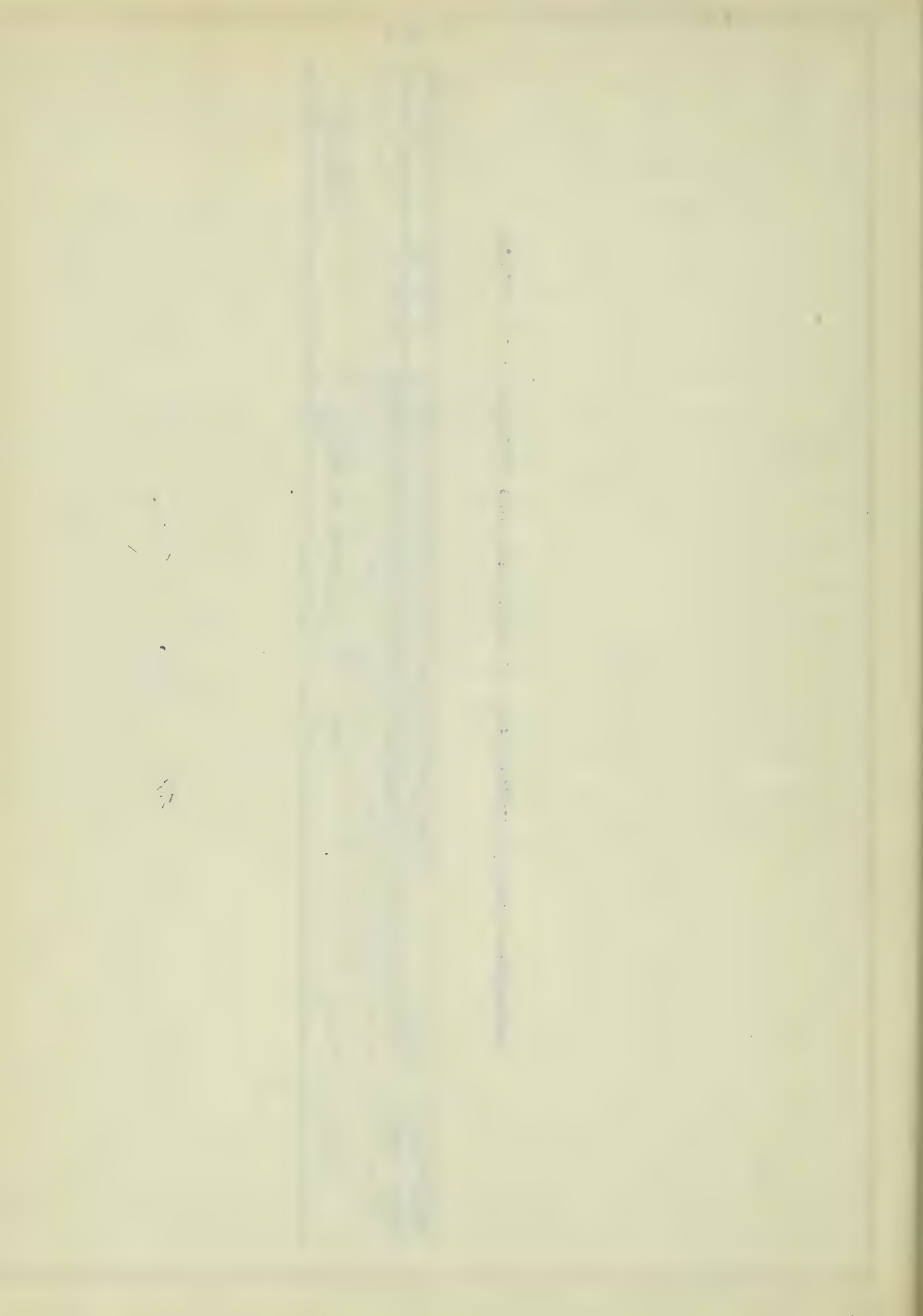
insertion in the inner layer of the same muscles whose fibers intertwine all the muscles of the circular and radial type, particularly at their origin and insertion.

This muscular bulb in most cases stands with the anterior end open thus forming a continuation of the funnel formed mouth opening to the posterior of the pharynx which is in all instances observed by the writer closed just anterior to the oesophagus which leads posteriad from this organ.

The oesophagus is a thin walled tube of varied length. In Cyclocoelum VN 15.65 it measures 0.347 to 0.463 mm. In Cyclocoelum VN 08.183, 0.331 to 0.662 mm. In Cyclocoelum VN 94.1, 0.483 mm on an average. The wide range of variation in length is due to the fact that the oesophagus takes an S-shape (Fig. 10) which is no doubt due to a state of partial contraction taken at fixation. This condition makes it impossible to secure the exact length of this organ. Because of the different states of contraction the oesophagus is more inflexed in some specimens than in others consequently a much greater variation in length. The following table exemplifies the condition mentioned above.

Name	Measurements in mm										Average	Range
	1	2	3	4	5	6	7	8	9	10		
Cyclocoelum VN 08.183	0.662	0.298	0.331	0.380	0.397	0.496	0.662	0.331	0.529	0.529	0.419	0.298-0.662
Cyclocoelum VN 08.180	0.496	0.413	0.331	0.596	0.546	0.298	0.662	0.413			0.469	0.298-0.596

Table II. - Showing the variation in the length of the oesophagus



In this case as previously stated the length varies from 0.298 mm to 0.662 mm making an average for the eleven specimens of 0.419 mm. Under the conditions mentioned above the average does not represent the actual length of the oesophagus. As will be noted from table II the oesophagus of individual number 1 is more than twice as long as that of individual number 2. However the maximum length of the oesophagus is not represented by the maximum measurements secured since in no case has the writer observed the oesophagus when it could be said to form a straight line from the oral sucker to the pharynx. The normal condition is represented in figure 10 where the oesophagus arises at the dorsal portion of the pharynx and from there takes a winding course both laterally and dorso-ventrally to the intestinal bifurcation into which it enters either directly from the dorsal or from the ventral sides respectively.

The Intestinal Crura. - As previously stated the intestinal crura usually bifurcate at the point of union of the oesophagus and the intestine, One branch passing to the right, the other to the left side of the body. Thus forming an arch which lies in the anterior one-sixth of the body. The crura extend from this parallel to the body wall, and are separated from it only by the vitellaria, to the extreme posterior end where they anastomose forming a posterior arch. This is separated from the posterior body wall by the excretory bladder. The crura are usually large with a large lumen (Plate I). However in some cases the crura are extremely irregular and show in some instances more or less distinct pouches (Fig. 2) which in some individuals appear as distinct diverticula and in fact are as strongly exemplified as some of those shown by

Stossich (1902) and Kossack (1911) for the genus Typhlocoelum. This feature however is not constant for any species of the genus Cyclocoelum observed by the writer and is probably due to the pressure produced by the expanded uterine loops which fill out the space between the crura and in many instances reach over the crura (Fig. 3). Anterior to the intestinal bifurcation in Cyclocoelum VN 08.180 and VN 08.183 there is an evagination which makes a pronounced undivided neck of the crura into which the oesophagus opens. (Fig.2) This is a constant character for these species and appears in a greater or less degree in every specimen of the fifty-six in the two collections. This is in decided contrast to the other species studied. (Compare Figs.1,2,&3).

III. THE POLYPHYLETIC ORIGIN OF THE MONOSTOMES

Historical. - From the earliest records of the Monostomata up to the present time this group of parasites has served for a dumping ground for inaccurately studied species which showed the slightest resemblance to the true Monostomes. Many species have since been studied more carefully and consequently have been transferred to other genera. Out of this has arisen the problem of the origin of the Monostomata based largely on the presence of what were termed by Cohn (1904) and Odhner (1907) rudimentary acetabula.

Cohn (1904) in his study of *Typhlocoelum* (*Monostomum*) *flavum* (Mehlis) worked over by Stossich (1902) and placed in the new genus *Typhlocoelum*, found a well developed but small ventral acetabulum which he figures from sagittal sections. This species on the one hand is apparently very closely related to the genus *Cyclocoelum* and was by Stossich (1902) placed in the sub-family *Cyclocoelinae*. On the other hand Cohn would transfer this to the *Fasciolidae* because of the presence of the ventral acetabulum which he says is diminished and in other instances often lost because of the shut in habitat under which these worms live.

He adds as was stated previously the observation of a rudimentary mouth sucker in *Cyclocoelum* (*Monostomum*) *mutabile* (Zeder) and in one other species of this group. Here he states that *Cyclocoelum mutabile* does not lack a primary sucker in many cases and like the Cestodarian *Amphilina* has lost holdfast organs because of the lack of need for such organs in the cavities of the body of the host in which habitat these worms live. According to this author *Cyclocoelum mutabile* (Zeder) and *Typhlocoelum flavum*

(Mehlis) are very closely related and that because of different stimuli in their respective habitats, alveolar spaces, abdominal cavity(?) and liver for Cyclocoelum and trachea and bronchi for Typhlocoelum that the ventral acetabulum of Cyclocoelum has been lost while the oral acetabulum of Typhlocoelum was atrophied.

In his earlier work (1902) the same author described *Monostomum oculobium* collected from *Vanellus melanogastrus* as having neither oral nor ventral acetabula and relates it to *Cyclocoelum mutabile* (Zeder). Fuhrmann (1904) describes a species, *Bothriogaster variolaris* collected from the intestine of *Rostrhamus sociabilis*, a South American Falconidae which from his figures and description appears to be very similar to *Monostomum oculobium* of Cohn (1902). He states here that in regard to the intestinal crura, absence of the oral sucker and the presence of only a pharynx it is like *Syclocoelum mutabile*. The position of the genital glands are not the same but on the other hand are like those of *Monostomum oculobium* of Cohn (1902). But differs from *Monostomum oculobium* Cohn in that a ventral acetabulum is present (*Bothriogaster variolaris*) which Fuhrmann believes Cohn has overlooked. Fuhrmann would place *Bothriogaster variolaris* in the subfamily Syncoelinae of the Fasciolidae.

Odhner (1907) supports the view of Cohn and sites a number of instances in its support. The most striking of which are cited here. Chief among these are, first, his genus *Aporocotyle* which he says he found first as an ecto-parasite and later as a blood parasite. This worm appeared usually singly, once two individuals another time seven individuals on the same fish (1900:63). He says that this suckerless form has its nearest relative in *Haplotrema constrictum* (Leared) a blood parasite of the Sea Turtle;

second, as stated before in this work those inhabiting the air sacs have developed the hold fast organs to the least degree. This includes the Cyclocoelidae which Odhner says are entirely suckerless except for the recent discovery of an entirely rudimentary ventral acetabulum in *Typhlocoelum flavum* (Mehlis) by Cohn (1904). He adds that in the Holostomes and Hemistomes the ventral acetabula have been greatly reduced and in some instances have disappeared entirely.

This author believes that the Monostomata will be finally split up entirely and added to other trematode groups, i.e. to the Distomes, Amphistomes, Holostomes and perhaps others.

Discussion. - Whether this is the correct interpretation remains indeed a matter of conjecture and certainly lacks much confirmation. It is difficult to ascertain from an anatomical study of adult forms alone as to whether these acetabula are vestigial. The most immature forms studied by the writer show no trace of such organs. These forms belong to *Cyclocoelum* VN.08.179 and *Cyclocoelum* VN 95.2, in these forms however the adults show no trace of a sucking organ. It is highly probable that a study of the life history of these forms would throw more light on this subject. So far as the writer is able to ascertain none of the cercariae of the genus *Cyclocoelum* have been recorded.

It is worthy of note however that in the Notocotylidae the oral sucker is well developed in the cercariae as well as in the adult, but instead of a single well developed sucker the condition is somewhat varied. In *Notocotylus quinqueserialis* five rows of small sucking discs are provided. In *Notocotylus triserialis* three rows of such organs are present, while in *Nudocotyle novicia* Barker (1916) no such sucking organs are present. These species

live in a similar habitat, intestines of the muskrat, and under this condition have developed in the first instances noted different numbers of these muscular organs while in the latter case none have been observed. *Nudocotylus novicia* however presents other striking differences and indeed may not belong to this genus. In the cercariae of these forms described notably by Cort (1915) and Faust (1917) no such organs are found nor is there any indication of their early development. The other organs of these larvae correspond to *Notocotylus* that there is no doubt as to the identity of the forms. In this case then the sucking discs are probable developed after the organism enters the definitive host. The final decision of this question however must await further evidence.

The cases of reduction of sucking musculature cited by Cohn (1904) and Odhner (1907 & 1911) are very interesting indeed and perhaps more striking because they are opposed by parallel instances where the worms have lived in secluded places of the host and still the suckers are well pronounced. For example *Schistosomum japonicum* which lives in the blood of the portal system has well developed acetabula both in the larval and the adult stages. Another old parasite which is shut in, in its habitat is *Opisthorchis felinus* and in this case the acetabula are again well developed. This parasite lives in the gall ducts of the liver of the host (birds, mammals and reptiles) and in the same organ of the snipe (*Gallinago delicata*) live members of the genus *Cyclocoelum* (*Cyclocoelum* VN 19, 26) . The latter species however shows no trace of sucking organs of any sort.

In contrast to the case cited by Odhner (1907) of *Typhlocoelum flavum* (Mehlis), about which he says the environment of the habitat has caused the oral acetabulum to atrophy while the ventral one

is retained, is not well substantiated since in the Heronimiidae which inhabit the lungs and especially the larger bronchi of turtles the oral acetabulum is well developed while any evidence of the presence of a ventral sucker has not been observed. This stands in rather striking contrast to the statement of Odhner (1907) referred to above.

Fuhrmann(1904) cites an interesting case in his *Bothriogaster variolaris* which was collected from the intestine of *Rostrhamus sociabilis*. This species according to this author has a ventral acetabulum but no oral acetabulum. A pharynx however is present. As stated previously this species is strikingly similar to *Monostomum oculobium* Cohn taken from *Vanellus melanogaster* which Cohn (1902) says is devoid of sucking apparatus. Why has the oral sucker of *Bothriogaster variolaris* atrophied if reduction is due to habitat as stated by Cohn (1902) and Odhner (1907) and (1911)? Certainly intestinal worms have need for hold fast organs. And why are not ventral acetabula developed in *Nudocotylus novicia* Barker?

As was stated previously Odhner (1901) proved beyond doubt the presence of both pharynx and oral sucker in *Didymozoon scombr* Tschbg. but found there no ventral sucker.

Four years later Ariola (1906) asserts the *Didymozoon* nature of *Kollikeria (Distoma) okeni* (Kölliker) which he states is synonymous with *Monostomum fillicolle* Rud. In the Parona material reported as *Kollikeria* in which there were many distomes according to this author, he finds a single form without the ventral acetabulum this he says is *Kollikeria okeni*.

On the other hand *Collyriclum faba* (Bremser) and *Collyriclum colei* Ward other cyst living trematodes, have no ventral acetabula

but present however a well developed oral sucker. It is difficult to interpret how worms which live under such similar conditions as the Didymozoonidae and the Collyriclidae could be affected by the habitat alone become so totally different.

Cohn(1904) gives Amphilina as a similar example of the loss of sucking apparatus because of the habitat in which it lives, yet on the contrary there are shown in other widely divergent groups striking resemblances developed under similar conditions as regards habitat. For example the Rhynchobothridae have developed four retractile probosces as holdfast organs while the Acanthocephala under practically identical habitat developed only one.

While the writer does not have a solution to offer at this time the one previously discussed is highly improbable and the final solution must necessarily await further accumulation of data and the bringing to light of new facts which bear upon this problem.



IV. CONCLUSIONS

1. That the pharynx is not a true sucker in the Monostomes as shown by the presence of both organs in two species of the genus Cyclocoelum.
2. That the loss of sucking or hold fast organs is not due to habitat alone.
3. Trematodes under practically identical conditions as to habitat take very different directions of development.
4. There is not yet sufficient reliable evidence accumulated to determine if the Monostomes are of Polyphyletic origin.

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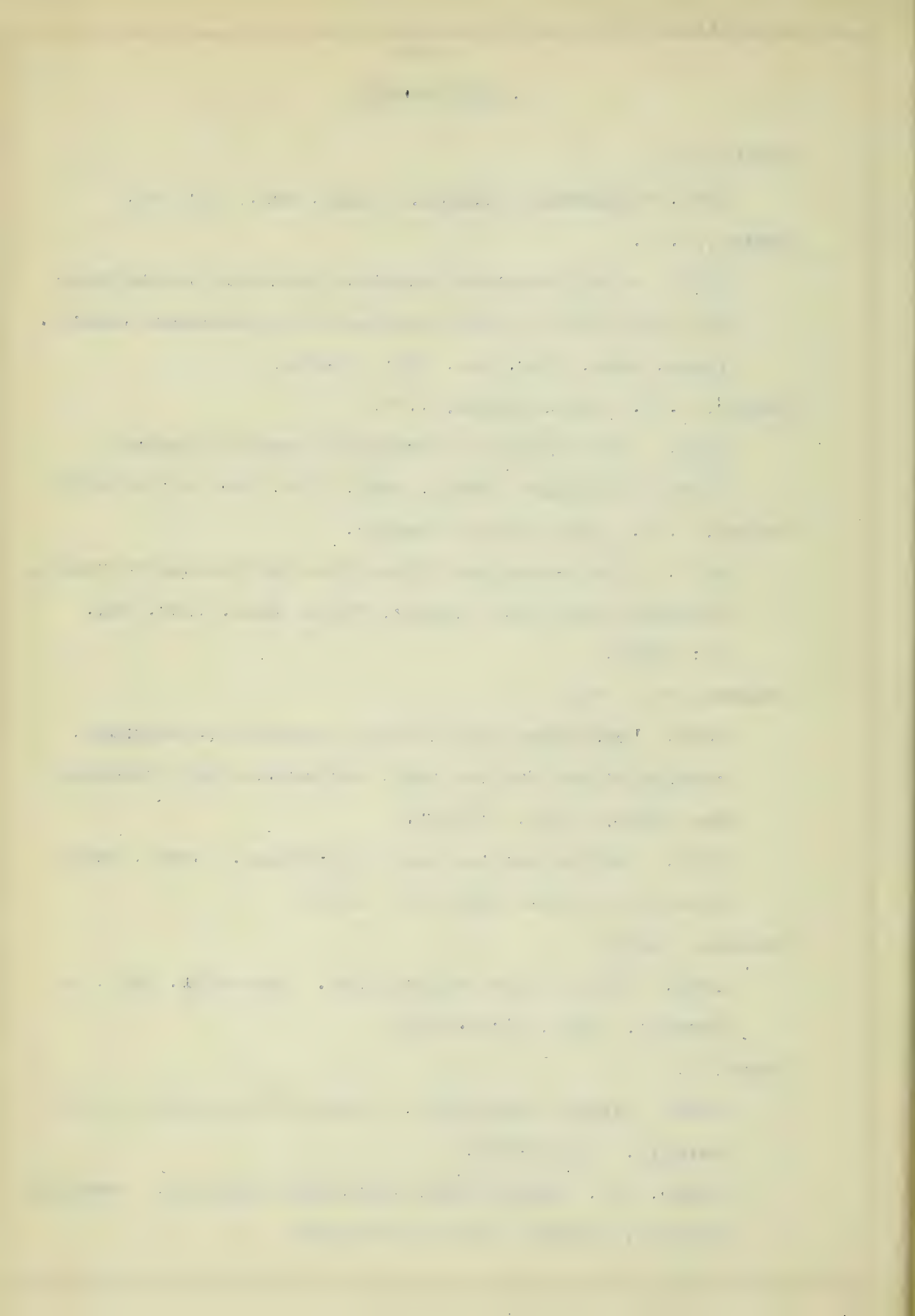
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VI. EXPLANATION OF PLATES

Abbreviations.

at - - - -anterior testis	ng - - - - nerve ganglion
b - - - - body wall	o - - - - oesophagus
c - - - - crura	om - - - - oblique muscle
cm - - - - circular muscle	os - - - - oral sucker
cp - - - - cirrus pouch	ov - - - - ovary
cu - - - - cuticula	ph - - - - pharynx
e - - - - eggs	pph - - - - prepharynx
ex - - - - excretory bladder	pt - - - - posterior testis
exp - - - - excretory pore	rm - - - - radial muscle
ext - - - - excretory tubules	rs - - - - receptaculum seminis
gp - - - - genital pore	rsu - - - - receptaculum seminis uterinum
l - - - - labium	tm - - - - transverse muscle
lm - - - - longitudinal muscle	u - - - - uterus
m - - - - mouth opening	vad - - - - vas deferens
mg - - - - Mehlis's gland	v - - - - vitellaria
nc - - - - nerve commissure	vd - - - - vitelline duct

Plate I. - Fig. 1. Cyclocoelum VN 15.65, dorsal view. x 14.

Fig. 2. Cyclocoelum VN 08.183, dorsal view. x 14.

Fig. 3. Cyclocoelum VN 94.1, ventral view. x 15.

Plate II. - Fig. 4. - Cross section of Cyclocoelum VN 94.1 through the posterior portion of the labium showing structure of mouth opening. x 108.

Fig. 5. - Cross section of Cyclocoelum VN 10.41 through the posterior portion of the labium showing the sucking musculature. x 108.

Figs. 6 & 7. - Cross sections through the mouth region of Cyclocoelum VN 15.65 showing the well developed sucking musculature. x 108.

Fig. 8. - View of anterior end of Cyclocoelum VN 15.65 showing sucker and pharynx in situ. Ventral aspect. x 53.

Fig. 9. - Frontal section through anterior end of Cyclocoelum VN 15.65 showing the relation of the oral sucker to the pharynx. x126.

Fig. 10- Drawing from wax reconstruction of anterior end of Cyclocoelum VN 15.65 showing the relative positions of the oral sucker, pharynx, oesophagus and intestinal caeca. Lateral aspect. x 130.

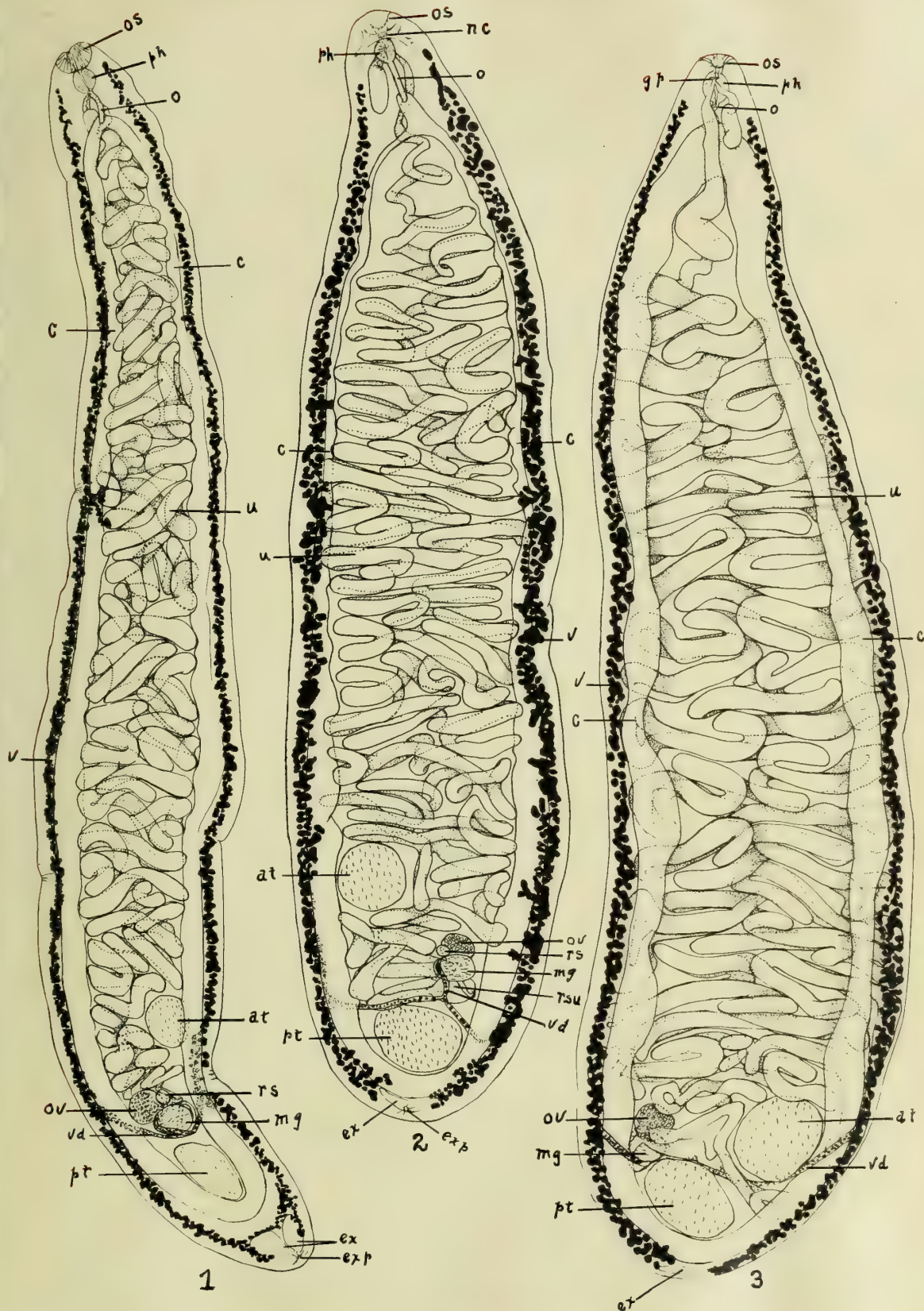


PLATE I

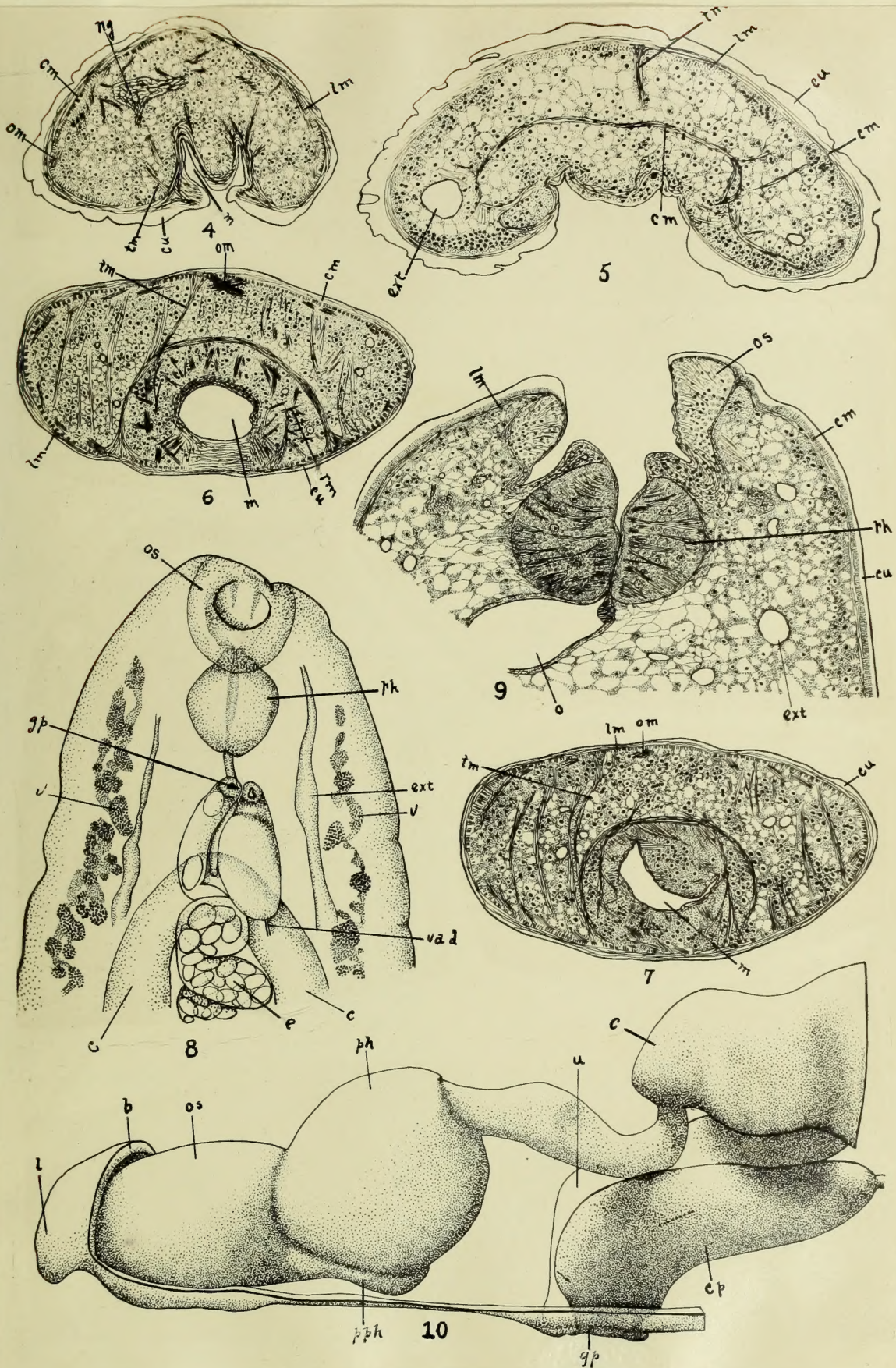


PLATE II

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